Abstract In this study we investigated the relationships between dominance rank and access to shelters in captive groups of *Lipophrys pholis* and *Coryphoblennius galerita*, as well as the effects of group size and shelter availability. Dominance rank was strongly correlated with size in juvenile *L. pholis* and with sex and size in adult *C. galerita*, males being dominant over females of similar size. Access to shelters was significantly correlated with dominance rank. For both species, most interactions occurred out of shelters. Direct disputes over shelters were always initiated by the dominant fish and the initiator was always the winner. The rate of aggression per fish per unit time decreased with an increase in the number of fish in *L. pholis* but not in *C. galerita*. No significant differences were found in groups differing in the number of shelters. *C. galerita* showed a higher rate of agonistic interactions and a higher proportion of overt aggression than *L. pholis*. It is suggested that one of the functions of agonistic interactions in these fishes is the control of a set of shelters, in the network of pathways used by each individual within its home range, minimizing the time required to hide in case of danger.

Keywords Agonistic behaviour · Dominance · Access to shelter · Diffuse territoriality · Intertidal fishes

Introduction

The presence of agonistic behaviour in rocky intertidal fishes has been a subject of interest for many years but its functional significance is still incompletely understood. Guitel (1893), a pioneering researcher on fish behaviour, first described aggressive behaviour and territoriality in the breeding males of several intertidal fish species, and Gibson (1968) demonstrated that juveniles of *Lipophrys pholis* (Linnaeus, 1758) possess a wide repertoire of agonistic behaviour. Other studies have reported the presence of agonistic behaviour in adult males of other species as well as in adult females and juveniles (e.g. Phillips 1977; Wirtz 1978; Almada et al. 1983, 1990; Mayr and Berger 1992; Gonçalves et al. 1996; Faria et al. 1998a). In his successive reviews on the behaviour of littoral fishes, Gibson (1969, 1982, 1986, 1988, 1999) summarised the available information on the subject.

In many cases, however, it is not fully clear for which resources the fishes are competing. Indeed, although it is known that the males of most intertidal fishes establish breeding territories (Almada and Santos 1995), a situation in which the functional role of agonistic behaviour is probably easy to understand, females and juveniles of many, and possibly most, species are non-territorial (e.g. Fishelson 1963; Almada et al. 1983, 1992, 1994; Santos 1985; Gonçalves and Almada 1998), a condition in which the function of agonistic behaviour is less obvious. In addition, feeding activities are often spread over a wide area covered by water when the tide rises (e.g. Hartley 1949; Gibson 1972; Almada et al. 1992; Gonçalves and Almada 1998), and the periods of lowest activity are at low tide, when the fishes are concentrated in pools and crevices (Gibson 1967, 1970, 1971, 1978). Thus, it remains unclear what adaptive consequences, if any, may result from agonistic behaviour clearly observed in pools at low tide as described by Almada et al. (1983) for *Coryphoblennius galerita* (Linnaeus, 1758) and *L. pholis*. Finally, although present in many rocky intertidal fishes, agonistic behaviour seems to be absent in several species that can reach high levels of aggregation without signs of aggression (several examples, mainly in cottids, can be found in Gibson 1982).

Gibson (1968), in the first study of the agonistic behaviour of juveniles of *L. pholis*, suggested that the fishes presented what he called “diffuse territoriality”, that is, instead of defending fixed territories, they could
defend the priority of access to shelter holes present in
their home range, although without controlling exclusive
use. Independently, Almada et al. (1983), based on
aquarium and field observations, suggested that intertidal
blennies, like C. galerita and L. pholis, used a network
of familiar pathways that included more than one shelter.
In their view, the fishes would compete not for a perma-
nent presence in a shelter, but for undisputed priority of
access to the shelters present in the neighbourhood of the
location where the fish is at a given moment, to mini-
mise the time during which the fish is exposed if a po-
tential predator appears in the area. This hypothesis was
based on three types of observations:
1. In tide pools, fishes disturbed by the observer often
followed the same pathways.
2. In their attempts to escape, fishes entered holes that
had been occupied by other fishes and one of them
was forced out.
3. When undisturbed, fishes were often seen in conspic-
uous positions, in salient topographic features of the
pools, but upon disturbance they dashed to shelters in
a multiplicity of distinct directions, as if each individ-
ual “knew” the shortest route to escape, leaving the
observer unable to track their diverse movements.

Other studies of rock intertidal fishes that provide evi-
dence that access to shelter is an important resource at
stake in agonistic encounters are those of Grossman
(1980), Behrents (1987), Koppel (1988), and Mayr and
Berger (1992). Faria et al. (1998b) partly tested this hy-
thesis, demonstrating that there is a significant corre-
lation between the dominance rank of each fish in a
group and the time spent in shelters. This correlation was
true for C. galerita and L. pholis, but not for Gobius co-
bitis (Pallas, 1814), another intertidal fish that lives in a
habitat poor in shelters like crevices and small holes suit-
able for single fishes.

In this article we further investigate the hypothesis
that access to shelter sites is rank dependent and con-
trolled by agonistic interactions, based on observations
of captive groups of L. pholis and C. galerita in tanks
where group size and shelter availability were manipu-
lated. To address this issue, we considered that it would
be necessary to study in more detail the character of the
dominance orders in the groups of each species and the
possible relationships between dominance and spatial
distribution of fishes outside shelters.

Methods

From October 1997 to May 1999, 32 groups of L. pholis and
C. galerita were observed in tanks of 118×28×27 cm. The tanks
were illuminated 10 h per day and were equipped with biological
filters. The temperature was 17°C. Fishes were fed with pieces of
common cockle. A total of 224 h of observation was made of the
32 groups, 16 of C. galerita and 16 of L. pholis. The observations
were based on groups of six fishes (8 groups of each species) and
four fishes (8 groups of each species), the fishes being 3–7 cm to-
tal length (TL). This size range was chosen to use fishes of com-
parable size. Because in this size range L. pholis are almost always
juveniles and C. galerita tend to be adults, individuals of C. gale-
rita with signs of being in reproductive condition were not used.
For each species group and density (six or four fishes), half of the
tanks were provided with two shelters (stones covered with algae)
and half with four shelters. Each group stayed in captivity for peri-
ods of 17 days, but no observations were made in the first 7 days
(habituation period). On subsequent days, daily observations were
made on 7 of the 10 remaining days, 1 h per day, randomly distrib-
uted from 0900 hours to 1900 hours. The habitation period of a
week was chosen since in previous studies (Almada et al. 1983;
Faria et al. 1998b), it was found that after 7 days the fishes moved
actively and interacted frequently with each other. We assumed
that these findings were indicators of habituation to the
conditions of captivity. In addition, a week is supposed to be a period suffi-
ciently long to minimise the influence of the tidal rhythm that
these fishes show in nature (Gibson 1967).

The fishes were recognised individually by their relative size
and the peculiarities of their colour patterns. For each fish, its lo-
cation in the tank was noted every 10 min during the observation
time (six scans per hour). The sequences of agonistic behaviour
that occurred during each hour of observation were recorded. A
fish was classified as the loser of an encounter if at the end of the
interaction it withdrew or fled from the opponent, or was threat-
ened or attacked without retaliation. When both fishes withdrew
without an apparent array, the outcome was classified as in-
conclusive. To make data from different groups comparable, the
size (TL) of each fish was expressed as relative size in relation to
the other members of the group. To calculate the dominance rank
of each fish in its group we followed the procedure described in
Appleby (1983). This calculation involves the computation of all
the interactions for each possible pair of individuals in a group. If
a member of the pair wins the majority of the interactions in
which the pair was involved, it is assigned a score of (+1); the
loser of most interactions is assigned a score of (0); if both mem-
bers of the pair were winners the same number of times, they are
both assigned a score of (0.5). The scores of each individual are
subsequently summed and individuals are finally ordered accord-
ing to their respective sum of scores. To analyse the spatial distri-
bution of agonistic encounters the bottom of the tank was divided
by an imaginary grid of 3×2 cells.

Statistical analysis was performed using the computer program
Statistica for Windows (v. 4.5, C. Statsoft Inc., 1993). The analy-
sis of contingency tables was performed using the simulation sta-
tistical procedure ACTUS (Estabrook and Estabrook 1989),
and the $\chi^2$ goodness-of-fit test was performed using the simulation
procedure Adersim (see Almada and Oliveira 1997 for details).
Both ACTUS and Adersim compare the observed values with a
collection of randomly generated, with probabilities proportional to the expected value of
each cell of the data set. These techniques have the advantage of
avoiding the limitations associated with the use of the chi-
quare distribution, allowing at the same time the assessment of the
significance of the individual cells of the data set.

The relationships between sex and rank and between size and
rank were analysed as described in Faria et al. (1998b). As this
procedure raises some peculiar problems it will be described in
some detail. These relationships were assessed using Spearman
correlations between relative size and rank and between sex and
rank, computed separately for each group. This raises some diffi-
culties: first, calculating correlations would not be the method of
choice to test relationships with dichotomous variables like sex;
second, the data are used twice to study the relationships of rank
with sex and size; and finally, with groups of small size, such as
six or four, only extreme values of correlations are significant. The
procedure is thus of low sensitivity. We decided to adopt it be-
cause, despite all these disadvantages, it has the advantage of
preserving the inter-group variability, allowing at the same time the
comparison of the associations of rank with sex and size with the
same statistic, in a situation in which more standard tests, such as
analysis of variance (ANOVA), would also be questionable. In do-
ing so we must stress, however, that it is not the statistical results
for each group that are relevant, but the repeated occurrence of the
same patterns across groups.